



11-2012

Neural Underpinnings of Prosody in Autism

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Recommended Citation

Eigsti, I. M., Schuh, J., Mencl, E., Schultz, R. T., & Paul, R. (2012). The neural underpinnings of prosody in autism. *Child Neuropsychology*, 18(6), 600-617.

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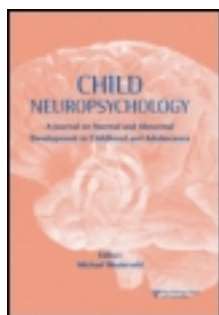
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Publisher: Psychology Press

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Child Neuropsychology

Publication details, including instructions for authors and subscription information:

<http://www.tandfonline.com/loi/ncny20>

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Available online: 19 Dec 2011

To cite this article: Inge-Marie Eigsti, Jillian Schuh, Einar Mencl, Robert T. Schultz & Rhea Paul (2011): The neural underpinnings of prosody in autism, *Child Neuropsychology*, DOI:10.1080/09297049.2011.639757

To link to this article: <http://dx.doi.org/10.1080/09297049.2011.639757>



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The neural underpinnings of prosody in autism

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This study examines the processing of prosodic cues to linguistic structure and to affect, drawing on fMRI and behavioral data from 16 high-functioning adolescents with autism spectrum disorders (ASD) and 11 typically developing controls. Stimuli were carefully matched on pitch, intensity, and duration, while varying systematically in conditions of affective prosody (angry versus neutral speech) and grammatical prosody (questions versus statement). To avoid conscious attention to prosody, which normalizes responses in young people with ASD, the implicit comprehension task directed attention to semantic aspects of the stimuli. Results showed that when perceiving prosodic cues, both affective and grammatical, activation of neural regions was more generalized in ASD than in typical development, and areas recruited reflect heightened reliance on cognitive control, reading of intentions, attentional management, and visualization. This broader recruitment of executive and “mind-reading” brain areas for a relative simple language-processing task may be interpreted to suggest that speakers with high-functioning autism (HFA) have developed less automaticity in language processing and may also suggest that “mind-reading” or theory of mind deficits are intricately bound up in language processing. Data provide support for both a right-lateralized as well as a bilateral model of prosodic processing in typical individuals, depending upon the function of the prosodic information.

Keywords: Autism; Prosody; Language; fMRI; Theory of mind.

While it is well known that individuals with autism spectrum disorders (ASD) have significant deficits in language abilities, there is ongoing debate about the nature of these deficits. In some of the earliest descriptions of ASD (Hermelin & O'Connor, 1970; Rutter, 1970, 1979), language was described as the primary domain of impairment, to which social impairments were secondary. Subsequent research reversed this emphasis, such that social impairments were conceptualized as primary and causally related to language impairments

We would like to acknowledge funding from NIMH P01 HD003008-38 (Project 3, Rhea Paul, PI); the work of Lauren Berkovits and Elinora Hunyadi; and the time and energy of the families who participated in this research.

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(e.g., Baron-Cohen, 1988; Mundy, Sigman, & Kasari, 1990). Prosody is an important aspect of language that may inform this debate, as it is centrally involved in both social and language functions. Unfortunately, behavioral studies of prosody in ASD are few in number and have yielded results that are generally at odds with clinical impressions. The current study focuses on the neural underpinnings of prosodic comprehension in ASD, examining the responses of adolescents with high-functioning ASD to both relatively social and relatively linguistic forms of prosody.

Prosody refers to the *pitch* (fundamental frequency), *intensity* (amplitude), and *duration* qualities of speech. Prosody has several functions, all of which make use of these same kinds of acoustic forms. *Grammatical prosodic cues* signal syntactic information, such as whether an utterance has a declarative (statement) or an interrogative (question) function. *Affective prosodic cues* signal the speaker's affective state (e.g., happy versus angry). As "suprasegmental" signals, these prosodic signals can be independent of the speaker's specific utterances (word choices or sentence structures); that is, an interrogative prosody can be uttered with a parallel interrogative linguistic structure (movement of an auxiliary verb to the start of the utterance, as in "Can I help you with that?") or with a declarative structure (as in, "Perhaps you need some help with that?"). Similarly, affective prosodic valances can be superimposed upon semantic meanings that might otherwise convey no particular emotion. In addition to differing forms of prosody, individuals must both produce and comprehend prosodic information; links between these two aspects of prosody are, to date, unclear.

Prosody in ASD

Since the first delineation of the autistic syndrome (Kanner, 1943), abnormal prosody production has been frequently identified as a core feature of the syndrome for individuals with autism who speak (Baltaxe & D'Angiola, 1992; Baltaxe & Simmons, 1975; Fay & Schuler, 1980; Ornitz & Ritvo, 1976; Paul, 1987; Pronovost, Wakstein, & Wakstein, 1966; Rutter & Lockyer, 1967; Tager-Flusberg, 1981). Differences noted in early observations of ASD included monotonic or machine-like intonation, deficits in the use of pitch and control of volume, deficiencies in vocal quality, and use of aberrant stress patterns. Speakers with high-functioning autism (HFA) demonstrate these difficulties (Ghaziuddin & Gerstein, 1996; Shriberg et al., 2001). Prosodic deficits have not been universally reported, however. Simmons and Baltaxe (1975), for example, found that only four out of the seven adolescents with autism they studied had notable suprasegmental differences in their speech. Paul, Shriberg, et al. (2005) reported abnormal prosody in 47% of the 30 speakers with ASD studied. When such behaviors are present, however, the prosody characteristics of a person with autism constitute one of the most significant obstacles to his or her social integration and vocational acceptance. Prosodic differences have been found to be persistent and to show little change over time, even when other aspects of language improve (DeMyer et al., 1973; Kanner, 1971; Rutter & Lockyer, 1967; Simmons & Baltaxe, 1975). Paul et al. (2005) report that prosodic differences are significantly related to ratings of ASD speakers' social and communicative competence. Moreover, Mesibov (1992) and Van Bourgondien and Woods (1992) reported that it is the vocal presentation of individuals with autism that most immediately creates an impression of oddness.

Given the salience of emotional and social deficits in ASD, most empirical research on prosody in ASD has focused on affective prosody, showing that prosodic deficits are linked to broader social emotional impairments. The research, in general, suggests the presence of deficits in comprehending affective prosody when individuals are asked to

label those emotions, or to match them to facial expressions of emotions (Boucher, Lewis, & Collis, 1998; Hall, Szechtman, & Nahmias, 2003; Schultz, 2005).

Studies of grammatical prosody, in contrast, have been somewhat less consistent. Individuals with autism show no particular impairments in the production (timing, length) or the comprehension of pauses (Fine, Bartolucci, Ginsberg, & Szatmari, 1991; Thurber & Tager-Flusberg, 1993), the production or comprehension of stress (Fine, et al., 1991; Paul, Bianchi, Augustyn, Klin, & Volkmar, 2008), the comprehension of utterance-final prosody (Fine et al., 1991), the production of pauses at grammatical boundaries in speech (Fine et al., 1991; Thurber & Tager-Flusberg, 1993), the use of unmarked (grammatical) stress placement (Fine et al., 1991), and the comprehension of stress and timing cues to grammatical phrase structure (e.g., “*chocolate cake* and cookies” versus “*chocolate, cake, and cookies*”; Paul, Augustyn, et al., 2005).

In contrast, however, some research *has* demonstrated significant impairments in prosodic or stress production in ASD (Baltaxe, 1984; Paul et al., 2008; Shriberg et al., 2001), particularly for speech that is more grammatically or semantically complex. Studies have revealed impairments in prosody for assigning contrastive stress (Baltaxe, 1984), grammatical placement of stress (Baltaxe & Guthrie, 1987), terminal pitch contours (Baltaxe, Simmons, & Zee, 1984), marking “chunks” of connected words during imitation (Fosnot & Jun, 1999), and comprehension of prosodic cues to phrase structure (Diehl, Bennetto, Watson, Gunlogson, & McDonough, 2008). A recent fMRI study of prosody in ASD indicated that processing of prosodic cues involved a failure of inhibition of the “default network” (Hesling et al., 2010), suggesting that individuals with ASD may be activating a distinct set of brain networks in comprehension.

While there have been a number of studies of prosodic comprehension and production in ASD, much of this literature is characterized by conflicting results, small sample sizes, and controls that are unmatched for age or IQ. In addition, many studies have relied upon explicit assessments. This is a significant methodological issue; data from a number of studies indicate that individuals with ASD often perform more similarly to controls when given explicit instructions, relative to spontaneous behavior. For example, the timing of spontaneous but *not* explicitly instructed facial mimicry is delayed in ASD (Charlop, Schreibman, & Thibodeau, 1985).

While studies of prosody in ASD have been inconclusive, it is clear that aspects of prosodic production and comprehension, particularly affective prosody, are perturbed in a significant proportion of individuals with ASD. Research making use of brain imaging may identify the neural processes underlying these aberrant behavioral patterns and may help to explain some of the phenotypic heterogeneity. In typical individuals, prosody is thought to depend on the recruitment of a large, complex, distributed network of brain regions (Robins, Hunyadi, & Schultz, 2009; Sidtis & Van Lancker Sidtis, 2003). In ASD, because prior studies suggest affective but potentially not grammatical prosodic impairments, we can ask whether this hinges upon difference in affective qualities. Alternatively, it may be the case that grammatical impairments are more difficult to characterize in sensitive tasks; thus, this approach offers the possibility of identifying important and salient clinical impairments in subtle linguistic skills in ASD.

Neural Bases of Prosody

Early research on the neural underpinnings of prosody drew on lesion studies and consistently demonstrated a right lateralization of emotional prosody and a left pattern of lateralization for grammatical prosody (Heilman, Leon, & Rosenbek, 2004; Van Lancker,

1980). More recent neuroimaging work in typically developing individuals has suggested three alternative hypotheses (Hesling, Clement, Bordessoules, & Allard, 2005). First, prosodic processes may draw heavily on subcortical regions (Cancelliere & Kertesz, 1990). Consistent with this suggestion, participants presented with filtered speech (containing no semantic information) display bilateral basal ganglia activation (Kotz et al., 2003). Second, prosody may be generally right-lateralized, with linguistic information processed in left hemisphere (Klouda, Robin, Graff-Radford, & Cooper, 1988). For example, fMRI studies that present participants with emotional valence versus phonological contrast decisions indicate bilateral involvement in both kinds of judgments, but relatively greater recruitment of right hemisphere for the emotion judgments, especially inferior frontal lobe (Buchanan et al., 2000). Third, prosodic processing may simply depend on specific acoustic cues (Van Lancker & Sidtis, 1992) and specific task demands (Luks, Nusbaum, & Levy, 1998). In general, posterior superior temporal regions are particularly important in prosodic processing and have also been highlighted as atypical across a variety of functional and anatomical studies of ASD (Just, Cherkassky, Keller, & Minshew, 2004).

In the present study, we used functional imaging to examine the processing of grammatical and affective prosody in youth (9–17) with HFA. In order to avoid conscious attention to prosody, which is likely to normalize responses in young people with HFA (Wang, Lee, Sigman, & Dapretto, 2006), we designed a task that focused attention on semantic aspects, while systematically varying the prosody of the stimuli. In this way, we aimed to investigate which brain areas would be recruited for prosodic processing when conscious attention was diverted. This approach will provide an opportunity both to evaluate the alternative hypotheses discussed by Hesling et al. as well as to look for ways in which this processing diverges from the normal pattern in speakers with HFA.

METHOD

Participants

High-functioning youth with and without ASD took part in a study of pragmatic and prosodic ability. Diagnostic assignment was made based on clinical consensus by a multidisciplinary team of experienced clinicians, using *Diagnostic and Statistical Manual of Mental Disorders*, fourth edition (*DSM-IV*, APA, 1994) criteria and making use of data from the Autism Diagnostic Interview-Revised (ADI-R; Lord, Rutter, & LeCouteur, 1994), the Autism Diagnostic Observation Schedule-Generic (ADOS-G; Lord et al., 1994), and clinical observation. Interrater reliability between these clinicians for diagnostic assignment was high, with kappa values ranging from .80 to .95 in related research projects. All participants were native, monolingual speakers of English, with normal hearing. Typically developing (TD) participants were included only if they had no history of learning or psychiatric disorders, based on parent report in the Childhood/Adolescent Symptom Inventory (Gadow & Sprafkin, 1997). They were between 9 and 17 years of age and had a Verbal IQ greater than 70 (on the Differential Abilities Scale [Elliott, 1990] for the ASD group or the Wechsler Abbreviated Scale of Intelligence [Wechsler, 1999] for the TD group). In addition, participants completed the Clinical Evaluation of Language Fundamentals (CELF), a standardized assessment of language skills (Semel, Wiig, & Secord, 2003), to determine overall language level.

Table 1 Demographic Information for Participants with Autism Spectrum Disorders (ASD) and Typically Developing (TD) Control Participants.

	ASD (<i>n</i> = 16, 14 boys)	TD (<i>n</i> = 11, 7 boys)
Age (years)	13.7 (2.8); 9 – 17	13.7 (2.6); 9 – 17
ADOS S+C ^{a***}	12.2 (5.7); 4 – 24	0.0 (0.0)
Full-scale IQ**	96.7 (14.9); 74 – 125	111.9 (10.9); 89 – 133
Verbal IQ	103.5 (22.2); 77 – 146	112.9 (9.8); 98 – 127
Performance IQ*	96.8 (15.7); 68 – 126	109.6 (14.5); 72 – 131
Handedness (R:L)	10:1	8:1
CELF Core Language (SS)*	97.4 (15.7); 69 – 120	110.1 (6.1); 100 – 123
CELF Expressive*	96.6 (15.0); 71 – 120	107.4 (6.3); 96 – 122
Behavioral prosody production and perception (accuracy)**	92.1 (4.7); 82 – 97	96.5 (1.9); 93 – 100

Note. Data presented as *M* (*SD*); range. Handedness was assessed using the PANESS inventory (Denckla, 1985). Not all participants completed a handedness assessment, due to experimenter error; data were missing for 5 participants in the ASD group and 2 in the TD group.

^aADOS S+C = Sum of scores on the ADOS Social and Communication domains (Modules 3 and 4); cutoff for ASD Diagnosis is 7.

TD > ASD: **p* < .05, ***p* < .01, ****p* < .001.

Sixteen children and adolescents with autism spectrum disorders (ASD; including 7 with Pervasive Developmental Disorder/Not Otherwise Specified (PDD/NOS), 5 with high-functioning autism, and 4 with Asperger syndrome) and 11 typically developing controls participated in this study. Typically developing controls were matched as a group to the ASD participants on the basis of chronological age and verbal IQ (all *F*s < 1.7, all *p*s > .20). Groups were also matched for gender, $\chi^2(1) = 2.15$, *p* = .14, and handedness, $\chi^2(1) = 0.117$, *p* = .73. Demographic data are summarized in Table 1. In addition, participants completed a behavioral assessment of prosody comprehension and production across four tasks; data are reported in a separate publication (Diehl & Paul, in press). While there were statistically significant differences between the ASD and TD groups on affective prosody perception, the participants with ASD were, nonetheless, correct on more than 87% of the items, indicating that they were able to comprehend and produce auditory cues relevant to prosody. All participants and caregivers gave informed consent.

Experimental Task

After training in a mock scanner and with the fMRI task, followed by screening to ensure safety, participants were placed on the bed of the scanner and provided with the button box. The head was stabilized with foam cushions placed inside the head coil. Participants wore MRI-compatible earphones and viewed the task through a mirror mounted on the head coil.

In the scanner, participants were presented with a series of sentences. The sentences (e.g., *It is five o'clock*; *She is typing fast*) were declarative statements, three to five words in length, consisting of high-frequency words (based on standard norms; Gilhooly & Logie, 1980; Kucera, 1967) and spoken by a female native speaker of English. Sentences fell into one of two affective conditions (Neutral or Angry emotion) and one of two grammatical

Table 2 Characteristics of Experimental Prosodic Stimuli by Condition.

	Pitch Pattern	Pitch Range
Neutral Statements	falling pitch	108.8–302.4
Neutral Questions	rising pitch	165.5–486.4
Angry Statements	falling pitch	127.7–338.5
Angry Questions	rising pitch	270.0–506.0

conditions (Statement or Question intonation), forming a two-by-two design. Across conditions, stimuli were matched on pitch, intensity, and duration, using Praat for manipulation of the acoustic signal, as shown in Table 2. Importantly, participants were *never* explicitly instructed to attend to the prosody of the sentences they heard. To maintain (and permit monitoring of) attention and to decrease explicit attention to the prosodic contrasts, participants were asked to report whether each stimulus sentence was about a living creature. The proportion of “yes” answers was set at 50%. To validate perception of the intended prosodic functions, university undergraduates rated audio recordings of the stimuli for the contrast between question and statement intonation ($n = 24$) and the contrast between angry and neutral ($n = 13$). Stimuli were only included when the ratings were at the appropriate end-points of the continua (either 4–5, or 1–2, along a 5-point continuum). The average affect rating (on a scale of 1 to 5, where 1 is completely neutral and 5 is completely angry) was 1.9 for the neutral sentences and 3.7 for the angry sentences. The average grammatical prosody rating (on a scale of 1 to 5, where 1 was clearly declarative and 5 was clearly interrogative) was 1.4 for the declarative sentences and 4.5 for the interrogative sentences.

Stimuli were presented in six runs with four different conditions (blocked) in a 2 (emotion prosody) \times 2 (grammatical prosody) design—(a) Neutral Statements; (b) Neutral Questions; (c) Angry Statements; (d) Angry Questions—in which emotional prosody was fully crossed with grammatical prosody by block. Each run included two blocks of each of the four experimental conditions (e.g., eight blocks), one block of an auditory attention control task (detecting a beep in noise) and a silent 10-second rest condition, for 11 blocks total in a pseudo-random order that maximized variability. There were 54 trials per run. Each block contained four 3-second trials with an intertrial interval of either one or two seconds (counterbalanced across trial types), and each block was followed by a 12-second rest trial.

Neuroimaging Data

MRI data were collected on a 3.0 Tesla Siemens Trio scanner at the Yale University School of Medicine Magnetic Resonance Research Center, with a standard birdcage head coil. Following localizer scans, 2D anatomical scans were acquired for in-plane coregistration with functional data (T1 flash, axial oblique plane through the AC-PC, 32 slices, 4 mm³ isotropic voxels with no gap between slices; TR/TE = 300/2.47, flip angle = 60°) with full cortex coverage and the first slice prescribed at “one slice above vertex” (top of brain). Six functional runs were acquired in the axial AC/PC plane, using a gradient echo, single-shot echoplanar sequence (TR/TE = 2000/20, flip angle = 80°, 32 slices, 4 mm³ isotropic voxels with no gap between slices). The final scan consisted of a 3D MPRAGE 1 mm³ anatomical image, also used for functional localization (176 slices,

1 mm³ isotropic voxels, TR/TE = 2530/3.66, flip angle = 7°). BrainVoyager QX 1.9 (Brain Innovation, Maastricht, The Netherlands) was used to analyze the recorded MRI data (Goebel, Esposito, & Formisano, 2006).

Preprocessing included intrasession alignment, motion correction, 7 mm FWHM Gaussian spatial smoothing, and linear trend removal. Five initial volumes per run were discarded. The functional image was coregistered to the 3D anatomical image, and the 3D image was then transformed into standard Talairach space using piecewise linear transformation. The Talairach and coregistration transformations were applied to the functional data to interpolate it into standard a 3D 3 mm³ space. All images are shown using radiological convention (e.g., the left hemisphere is on the right side of the image). Parametric maps were obtained using a general linear model (GLM) with multiple conditions. Analyses examined specific task contrasts using the *t* statistic. For whole-brain analyses, a conservative threshold of $p < .001$ was used to account for multiple comparisons. We examined activations as a function of grammatical prosody (question versus statement blocks, collapsing emotional prosody conditions) and emotional prosody (angry versus neutral blocks, collapsing grammatical prosody). Across subjects, random effects analyses of covariance (ANCOVAs) with CELF Core Language scores as a covariate tested differences in response to these stimulus types by group (ASD vs. TD).

RESULTS

Behavioral Analyses

Analyses of the behavioral task revealed that the ASD and control groups performed similarly in regards to correct performance on the explicit semantic task of determining whether each stimulus contained a living creature. A repeated-measures analysis of variance (ANOVA) on Condition \times Group indicated no group differences in accuracy across four prosody conditions, $F(1, 26) = 1.78, p = .19$, (ASD group: $M = 0.733, SD = 0.04$; TD group: $M = 0.814, SD = 0.05$). Similarly, groups did not differ in reaction time across conditions, $F(1, 26) = 1.39, p = .25$ (overall ASD group: $M = 1927, SD = 178$; TD group: $M = 2009, SD = 186$). Because of significant or near-significant differences in fundamental language abilities as a function of group, CELF Core Language scores were included as a covariate in all analyses.

MRI Results

In order to determine the neural regions involved in perception of prosody, we contrasted activations in response to the four prosody conditions, collapsing over group, using a random effects ANCOVA with Core Language scores as a covariate. There were multiple regions of activation, indicating that the prosodic contrasts recruited topographically distinct brain structures. To map out regions of activation more specifically, a series of analyses examined the main effect of emotional prosody on brain responses (angry versus neutral conditions) and the main effect of grammatical prosody (questions versus statements), collapsed across group. First, the Angry-Neutral contrast was reflected by significant regions of activation, including medial frontal gyrus ($X, Y, Z = 6, 38, 38$); left inferior frontal gyrus; and right precuneus ($12, -61, 29$). The Question-Statement contrast was reflected by significant activation in left superior temporal gyrus ($-53, 8, -2$). There was a significant interaction between group status and condition, reflecting regions

Table 3 Brain Regions of Significant Activation Induced by Affective Prosodic Contrasts in Participants with ASD and TD.

Type of analysis of variance and contrast	Brain region	Brodmann area	Talairach X,Y,Z coordinates
Between-group comparison			
Greater activation in TD than ASD (Angry Statements+Questions)	L IFG	47	-54, 23, -8
	Bilat parahippocampal gyrus		16, -8, -19
Greater activation in ASD than TD (Angry Statements+Questions)	L globus pallidus		-14, -6, -6
	R MFG		5, 45, 37
	R STG	6	30, 10, -20
	R Precentral Gyrus	4	54, -12, 41
Within-group comparison			
Activation reflecting emotional prosodic contrast in ASD (Angry - Neutral)	R MFG	10, 6	3, 52, 1 and -3, 37, 37
	L IFG	46	-46, 35, 11
Activation reflecting emotional prosodic contrast in TD (Angry - Neutral)	R STG	38	42, 10, -27

Table 4 Brain Regions of Significant Activation Induced by Grammatical Prosodic Contrasts in Participants with ASD and TD.

Type of analysis of variance and contrast	Brain region	Brodmann area	Talairach coordinates X,Y,Z
Between-group comparison			
Greater activation in TD than ASD (Questions)	R STG	22	46, -6, -6
Greater activation in ASD than TD (Questions)	Bilat Mid FG	10, 6	39,50,10; -26,2,47
	R ACG		2, 37, 29
	R SFG	6	15, 21, 53
Within-group comparison			
Activation reflecting grammatical prosodic contrast in ASD (Quest - Statement)	R Mid FG	10	43, 47, 13
	L STG	-	-39, 9, -13
	L ACG (decrease)	32	-5, 32, -4
Activation reflecting grammatical prosodic contrast in TD (Quest - Statement)	L Mid FG	46	-48, 30, 21
	L STG	22	-50, -7, -2
	L Fusiform	19	-39, -79, -12

of differences in activation, including right medial frontal gyrus (37, 49, 11), right inferior temporal gyrus (62, -16, -16), right parietal postcentral gyrus (5, -39, 63), right middle temporal gyrus (62, -41, 2), and left middle temporal gyrus (-44, -61, 27). Results, broken down by group, are presented in Tables 3 and 4.

Affective Prosody Results

To test the interaction of group status and specific affective and grammatical contrasts, additional analyses examined within-group and between-group contrasts by

condition; data are displayed in Tables 3 and 4. Groups differed in responses to Angry Statements and Questions. The TD group had significantly stronger activation in a single region, left inferior frontal gyrus (IFG), a region generally associated with higher level comprehension processes (e.g., Cooper, Hasson, & Small, 2011), as shown in Figure 1. In contrast, the ASD group exhibited significantly greater activation across multiple regions, including bilateral and right-localized regions, including right medial frontal gyrus, right superior temporal gyrus (STG), bilateral parahippocampal gyrus, right precentral gyrus, and left globus pallidus. In addition, the ASD group had left-lateralized activations for this prosodic contrast in IFG.

Grammatical Prosody Results

Examining activations in response to grammatical prosody (Neutral and Angry Questions), results indicated that the TD group had relatively greater right-lateralized responses in STG to the prosodic condition than did the ASD group. In contrast, the ASD group had stronger responses in the right anterior cingulate, right superior frontal gyrus, and bilateral middle frontal gyrus, as shown in Figure 2. The contrast between statements and questions, within the ASD group, indicated significantly greater activation in the right middle frontal gyrus, left STG, and left anterior cingulate. For the TD group, activations in response to the grammatical prosody distinctions were significant in the right middle frontal gyrus and left STG but also in the left fusiform.

DISCUSSION

The present study examined the neural characteristics of prosody perception in children with ASD and typical development, contrasting affective and grammatical forms of prosody. Given the conflicting behavioral results from studies of grammatical prosody in ASD, one primary goal was to investigate group differences in processing this form of prosodic information. A related goal was to understand the role of neural processes in underlying prosodic deficits, with the hope of clarifying whether distinct forms of prosody function similarly. Participants with ASD or typical development, matched on age, gender, and verbal IQ, completed an implicit prosody task, in which they made semantic judgments about a series of sentences in the scanner. Standard language assessment scores (CELF-Core) were included as a covariate in all MRI analyses.

Results from the semantic judgment task indicated that groups performed the explicit task with similar speed and accuracy, suggesting that they were equally attentive and engaged. In contrast to this similarity in behavioral performance, imaging results indicated salient group and condition-specific differences. Across groups, there was a main effect of condition, showing significant left-lateralized in addition to right-lateralized activation, which indicates that prosody is not straightforwardly a right-hemisphere-dominated process and rather is subserved by a complex, bilateral network of subcortical and frontal structures. Across groups, the affective prosody contrast elicited activations in language-critical regions (left IFG) reported to be involved in the processing of prosodic perception and production and correlated with affective empathy (Aziz-Zadeh, Sheng, & Gheyntchi, 2010) and sarcasm (Uchiyama et al., 2006) as well as more posterior regions (e.g., right precuneus) implicated in the brain's default network (Cavanna, 2007). Main effects of the grammatical prosody contrast, across groups, indicated activations of the left STG, part

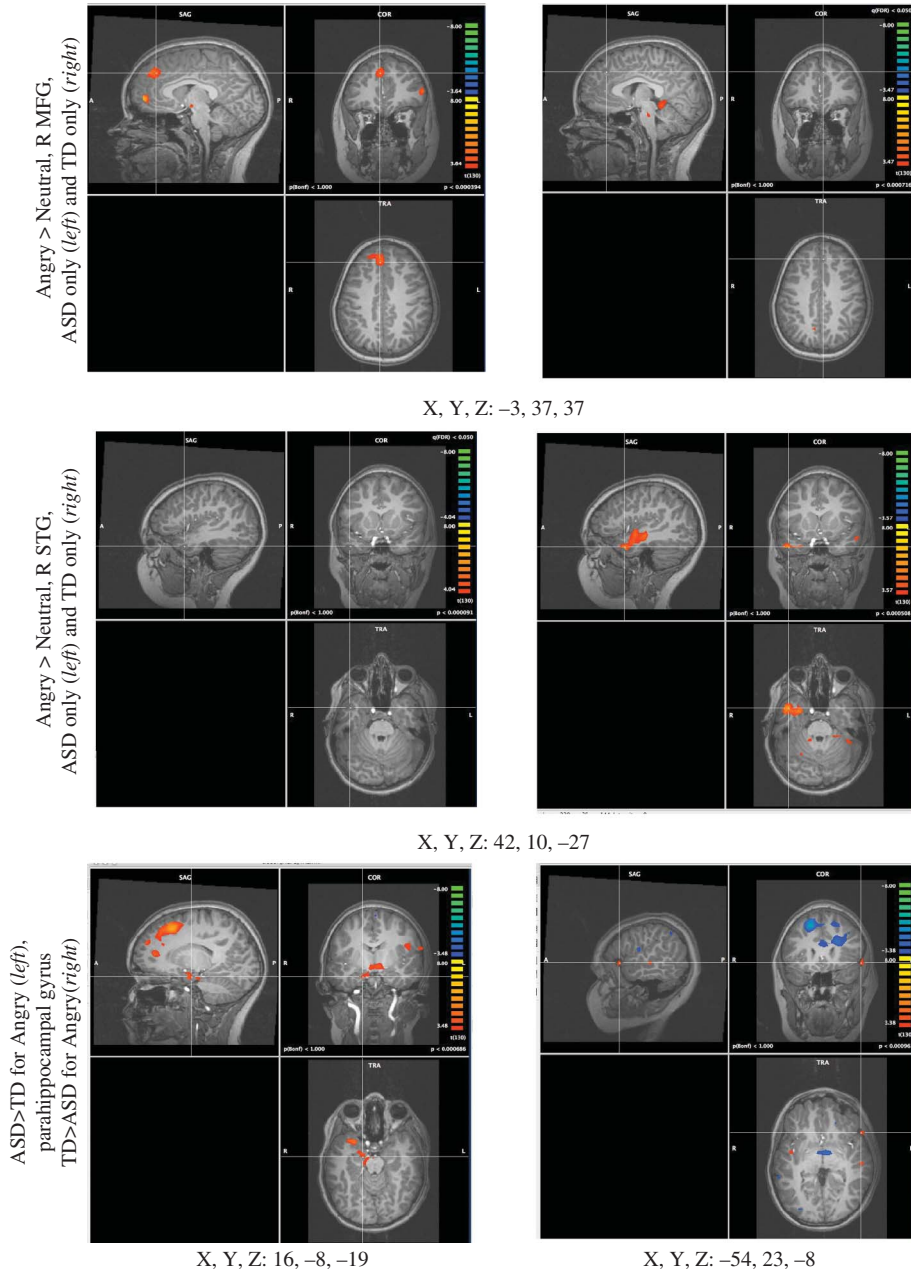


Figure 1 Brain regions of significant activation induced by affective prosodic contrasts in participants with ASD and TD.

Note. Activation maps for the ASD and TD groups obtained by comparing responses while listening to angry and neutral prosodic stimuli and making semantic judgments. Each panel shows significant foci of activation in both groups, in sagittal (top left), coronal (top right) axial (bottom) sections through stereotaxic space of activation maps superimposed onto representative brain anatomy. Stereotaxic coordinates (mm) are derived from the Talairach human brain atlas.

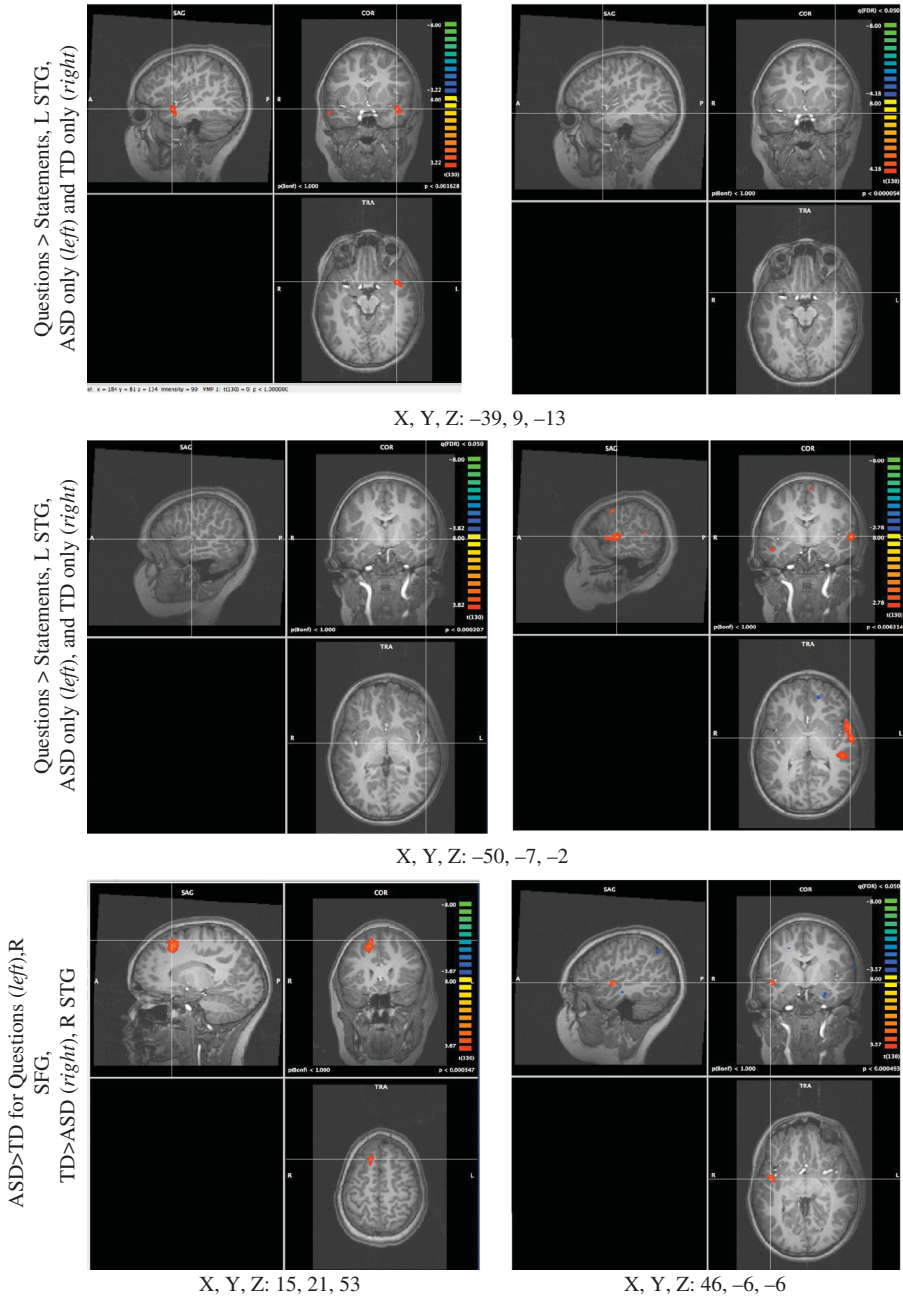


Figure 2 Regions of significant activation induced by grammatical prosodic contrasts.

of primary auditory cortex and often involved in language processes, including prelexical aspects of speech perception (Price, 2010).

Further Group \times Condition analyses, focusing on responses of TD group participants, confirmed prior results indicating right lateralization of emotional prosodic cues (e.g., to right STG) and left-lateralized activations for grammatical prosodic cues (e.g., left STG), providing support for models of prosody suggesting hemispheric lateralization of distinct forms. Thus, data from the present study support both a right-lateralized as well as bilateral aspects of prosodic processing, depending upon the function of the prosodic information.

The analyses of group contrasts somewhat complicates this picture. Comparison of group patterns of performance for prosodic cues indicated distinct patterns for both affective and grammatical contrasts, suggesting a significantly different network underlying cue perception in ASD. For affective cues, participants with TD had relatively stronger activation in left IFG, a region associated with language comprehension, and particularly activated in prior studies involving prosody, empathy, and sarcasm (Aziz-Zadeh et al., 2010; Uchiyama et al., 2006). In contrast, participants in the ASD group had significantly more activation in multiple regions, including bilateral parahippocampal gyrus, potentially reflecting memory demands, or perhaps reflecting the active visualization of scenes described in task stimuli (Epstein, 2008). Participants with ASD also had greater activation in left globus pallidus, a region involved in language-relevant cognitive control (Liu, Hu, Guo, & Peng, 2010), suggesting the harnessing of more attentional control resources as they perform the comprehension task. Participants with ASD showed significant right hemisphere activations in right STG (the left homologue of which is critical in language comprehension, and an area often invoked in prosodic processing) and in right MFG, a region involved in making inferences about others' intentions (Mason & Just, 2011). Finally, activations were greater in precentral gyrus (important in motor planning and sometimes in language comprehension; Price, 2010).

There was not sufficient power to analyze effects as a function of ASD diagnostic status (that is, contrasting autistic disorder, PDD/NOS, and Asperger syndrome). Certainly, this represents an opportunity for further research, given the heterogeneity in language skills that is present across diagnostic subtypes. That said, the current results held when CELF Core Language standardized scores were entered as a covariate for fMRI analyses; this suggests that differences in patterns of brain activation were not driven solely by the lower functioning end of the ASD spectrum. Furthermore, results from an extended behavioral assessment of a larger group of children and adolescents with ASD, of which the fMRI group presents a subset, indicate that language abilities (as measured by standardized scores on the CELF and the Children's Communication Checklist, second ed., described in Bishop, 1998) were more closely associated with prosodic difficulties than either IQ scores or diagnostic subtype (Diehl & Paul, 2011). Indeed, this result appears to be consistent with the decreasing importance of diagnostic subtype distinctions in the field (American Psychiatric Association, 2011).

In general, contrasts between the ASD and TD groups for the affective prosody conditions indicated significantly more regions of activation in the ASD group, as well as the activation of regions potentially implicated in cognitive control, visualization, and some aspects of inference about mental states and intentions. It should be noted that the portion of right STG activated significantly more by the ASD group maps onto coordinates of the right temporoparietal junction (TPJ) region, identified in prior studies "theory of mind" and mental inferencing tasks (Saxe & Wexler, 2005).

On one hand, the activation of right TPJ regions might suggest that individuals with ASD are “mentalizing” during prosody perception; that is, they might experience difficulty in interpreting the speaker’s communicative intent in processing the angry emotional cues. However, this brain region has also been implicated in lower level (bottom-up) computational processes involved in attentional reorienting (Decety & Lamm, 2007), as well as in service of maintenance of cognitive processes — keeping information “on line” (Ferstl & von Cramon, 2002). As such, greater involvement of this region in processing affective prosodic information could indicate that participants in the ASD group experience a relatively greater difficulty in orienting attention to salient, relevant components of the stimulus; this suggestion is consistent with prior work suggesting that when individuals with ASD are not explicitly told to direct their attention in prosodic comprehension, they perform significantly worse (Wang et al., 2006). That is, participants with ASD may fail to understand the *irrelevance* of prosodic cues to their explicit behavioral semantic judgment task and may devote disproportionate resources to this irrelevant but salient information. Alternatively, when attending to semantic cues, they may be struggling to disengage from prosodic cues, a finding consistent with prior research in which participants with ASD were unable to attend to prosodic cues when those cues conflicted with syntactic information (Diehl et al., 2008).

In response to the grammatical prosody distinction, TD participants exhibited significantly more activation in a single region, the right STG (characteristically involved in prosodic production and perception). In contrast, the ASD group showed activations across multiple regions, including those involved in error detection and cognitive control (right anterior cingulate cortex), cognitive control aspects of language (right superior frontal gyrus) often seen in bilingual language processing (Jamal, Piche, Napoliello, Perfetti, & Eden, 2011), and bilateral middle frontal gyrus. There was overlap for activations in a within-group analysis, but significant differences when groups are compared directly, particularly in regions associated with error detection and effortful control; in this case, the ASD group had significantly greater activation of these regions.

In general, findings suggested that individuals with ASD activated substantially more regions in the course of prosodic perception. Consistent with many other findings that “expertise” is associated with a reduction in activation (Aizenstein et al., 2004; Church, Coalson, Lugar, Petersen, & Schlaggar, 2008; Petrini et al., 2011), this suggests that adolescents with ASD utilize greater processing power during a straightforward linguistic task. During language comprehension, a listener rapidly makes incremental adjustments and uses multiple sources of information to resolve ambiguities (Snedeker, 2008); this demanding process may simply require more cognitive effort and attentional resources in individuals for whom language comprehension may be less efficient (e.g., Eigsti & Bennetto, 2009). This is consistent with better performance in explicit prosody tasks, when individuals know where attention and cognitive resources need to be directed, but worse performance in implicit tasks when participants must determine where to focus attention and are processing multiple levels of information (Paul et al., 2005).

The current results suggest some mechanisms (excessive cognitive control, greater resources dedicated to processing prosody, or greater overlap in processing grammatical as compared to affective prosodic cues) that may relate to prosodic impairments. Due to the implicit nature of the task, it is not possible to know whether participants were attending to prosodic cues, though the striking pattern of differential responses to the prosodic conditions suggests they were. Observed atypical patterns of activity in the ASD group could reflect domain-general difficulties in processing multiple levels of language or marshalling

attention to relevant aspects of linguistic stimuli that are not specific to prosody. Studies that contrast various levels of linguistic information, such as syntactic versus semantic or syntactic versus prosodic, could clarify this possibility.

The present study extends the small literature on neural processing of prosody in ASD. It suggests that, at least for tasks in which processing of prosody is implicit, activation of neural regions is more generalized in ASD than in typical development, and areas recruited appear to reflect heightened reliance on cognitive control, reading of intentions, attentional management, and visualization. This broader recruitment of executive and “mind-reading” brain areas for a relative simple language-processing task may be interpreted to suggest that speakers with HFA have developed less automaticity in language processing. Whether a deficit in automaticity is the result of inherently inefficient networks or limited experience due to a lifetime of attenuated responses to speech input, the current paradigm cannot disambiguate. Certainly, these possibilities are not mutually exclusive. Research that contrasts a range of implicit and explicit language-processing demands and compares younger individuals for whom development is ongoing would help to answer these questions.

Original manuscript received June 24, 2011

Revised manuscript accepted September 18, 2011

First published online December 16, 2011

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